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Running head: *Supplementary feeding of breeding Buzzards*

Supplementary feeding increases Common Buzzard *Buteo buteo* productivity, but only in poor quality habitat

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Temporal heterogeneity in the effects of food supply during the breeding season on the productivity of the Common Buzzard *Buteo buteo* was investigated in a supplementary feeding experiment. Pairs were fed artificially (1) before egg laying, (2) after chicks hatched and (3) continuously throughout the season and compared to (4) unfed controls. Pairs fed *before* egg laying had marginally larger clutches (+0.6 eggs more) than those not fed, but lay date, egg volume and weight, brood size and hatching success were unaffected. Territorial quality had far greater effects, with pairs nesting in low quality habitats (bog, scrub and semi-natural grassland) laying later, having lower hatching success, smaller broods and fewer fledglings than those in more productive agricultural landscapes. Supplementary feeding *after* egg hatching neutralised the negative effect of poor habitat resulting in fed birds having significantly more fledglings. This study emphasises the importance of food availability when provisioning chicks in sub-optimal habitats and has implications for the success of 'diversionary feeding' in reducing game-keeper losses to Buzzards (e.g. released pheasants).

Keywords: bird of prey, breeding season, food, human-wildlife conflict, reproductive success.

Food dictates the amount of energy available for self-maintenance, growth and reproduction, and thus directly affects fitness (Lack 1954, Martin 1987). However, other ecological factors, including weather, predation, competition and individual experience modify the immediate importance of food supply as a limiting factor on fitness (Krüger 2004, Robb *et al*. 2008).

The relationship between food availability and breeding success is important in wildlife management and has been tested frequently (see Newton 1998, González *et al.* 2006, Margalida 2010). As different stages in the breeding period require varying energy inputs, and food availability fluctuates temporally, the influence of food may change throughout the season (Lack 1954, Robb *et al.* 2008). However, the interaction between food supply and stage of breeding is investigated infrequently (Gill & Hatch 2002).

The importance of food during the breeding season has been tested in supplementary feeding experiments (e.g. Newton 1998). Often food added during the pre-laying stage increases clutch size and brings forward laying date, most notably when territory quality or natural food availability is poor (Newton & Marquiss 1981, Dijkstra *et al.,* 1982, Nager *et al.,* 1997). Although similar studies have contradictory results, many suggest that an increase in clutch size does not necessarily translate to an increase in number of fledglings (Newton & Marquiss 1981, Korpimäki & Wiehn 1998, Millon *et al*. 2008). In addition, food provided during the post-hatching stage can influence the success of inexperienced pairs and those in poor quality habitats (González *et al*. 2006, Byholm & Kekkonen 2008).

At the western-most fringe of its range, the Common Buzzard *Buteo buteo* population is recovering and expanding following extirpation during the late-19th to mid-20th centuries (Balmer *et al*. 2013), increasing concern about their impact on prey species, particularly those of commercial interest such as game birds (Lees *et al*. 2012). In addition, prey assemblages in part of the Buzzard's range are changing due to introductions of non-native small mammals (Rooney & Montgomery 2013). To test the effects of prey availability throughout the breeding

season on the number of fledglings produced, we conducted a pilot supplementary feeding experiment on free-living Buzzards. Moreover, since natural food availability is likely to vary with habitat, we examined the effect of habitat composition around the nest-site and its interaction with supplementary feeding pre-egg laying and post-hatching. We hypothesised that if food availability is the sole driver of reproductive success, pairs fed continuously throughout the breeding season should have higher reproductive output, especially in poor quality habitats.

METHODS

The experiment was carried out between March and August 2011 in north-east Ireland (54°N, 5°E) in an area 1,600km^2. The study area was composed principally of agricultural land (68%) including improved grassland and arable interspersed with low productivity natural habitats (20%) including bog, scrub and semi-natural grasslands as well as broad-leaved woodlands and conifer plantations (8%) or urban areas (3%). Forty Buzzard nest sites were located through vantage point surveys and were randomly assigned to one of four treatment groups; (1) fed *before* egg laying, (2) fed *after* chicks hatched, (3) fed continuously throughout the breeding season and (4) unfed controls. All pairs had been monitored a minimum of one year prior to the experimental study, and there were no sub-adult individuals identified, based on plumage. However, to minimise the effects of age/experience on the experiment all pairs were randomly assigned to treatments. A minimum of 35 days experimental feeding was conducted before egg laying in treatment groups 1 and 3 and 30 days after hatching in groups 2 and 3.

Food was provided on a 'T' post erected <30m from the nest. Posts were observed until the prey was seen to be taken by one or both territorial adults. Twenty-six breeding pairs consumed food readily and were used in the experiment. Every two days, beginning on the 1st March,

either one Rabbit *Oryctolagus cuniculus* (*c*. 1,000g) or two Woodpigeons *Columba palumbus* (*c*. 450g per item) were provided. Both prey species are consumed regularly by Buzzards in the study area (Rooney & Montgomery 2013). The prey type provided on each occasion was randomised. Although pigeon and rabbit differ in calorific content, both represent significant extra food in territories in experimental treatments.

Nests were visited shortly after the incubation period started, during which clutch size, mean egg weight (g) and volume (mm^3) were calculated following Hoyt (1979). Nests were revisited approximately 30 days later to determine hatching success (the proportion of eggs hatched) and early brood size (the total number of chicks hatched). Brood size measured at <5 days was assumed to reflect the number of chicks hatched, rather than the number of chicks remaining after brood reduction events (i.e. starvation or siblicide), given that these events in Buzzards occurs most often in the second to fourth weeks of the nestling period (Tubbs 1974), and that siblicide in raptors in general occurs most often when young are not being brooded (Newton 1979). Hatching date, if not observed directly, was estimated from the stage of development of the oldest chick, which was always <5 days old. Initial laying date at each nest was back-calculated as 35 days prior to hatching of the eldest chick in that nest (Tubbs 1974).

Whilst the experiment was designed as a four-level factorial treatment, variables measured *before* hatching could not have been affected by supplementary feeding *after* hatching. Therefore, where the effect of treatment on laying date, clutch size, egg volume, egg weight and early brood size was examined, the two treatment groups fed before egg laying were combined (groups 1 + 3 = 'pre-fed'), as were the two treatment groups not fed before egg laying (groups 2 + 4 = 'not pre-fed'). Similarly, where the effect of treatment on the number of fledglings was examined, those groups fed *after* hatching were combined (groups 2 + 3 = 'post-fed') as were the two treatments groups not fed after hatching (groups 1 + 4 = 'not post-fed') to create a second two-level factor. This allowed the independent effects of supplementary

feeding before-and-after egg laying to be examined whilst their interaction effect (i.e Pre-fed*Post-fed) was used to assess their joint contribution to the number of fledglings. Chicks were considered as successful fledglings on a final visit to the nest a minimum of 28 days after hatching (Hardey *et al*. 2009). Visits were only carried out in mild, calm weather to minimise disturbance

CORINE landcover type (EEA, 2010) was extracted within a 1km buffer around each nest using ArcGIS 10 (ESRI, California, USA). Variation in the coverage of improved grassland, arable, bog, scrub, semi-natural grassland, broad-leaved woodland, coniferous plantation and urban habitat was reduced by Principal Components Analysis (PCA) with varimax rotation onto a single component axis describing 'natural landscapes'. This was positively associated with bog and scrub (weighting = 0.835) and semi-natural grassland (weighting = 0.822) and represented 22.6% of landscape variation (eigenvalue = 1.259). There was no confounding effect of PCA scores on treatment (Supporting Information Fig. S1).

Lay date, mean egg volume and weight and hatching success were examined using a Generalized Linear Model (GLM) assuming a normal error distribution (tested for *a priori* using Kolmogorov-Smirnov tests) and an identity link function, fitting the two-level factor Pre-fed (yes/no), Habitat (PCA scores) and their interaction (Pre-fed*Habitat). Clutch size and early brood size were examined using identical GLMs but assuming a Poisson error distribution (for count data) and a logit link function. Number of fledglings was also examined using a Poisson GLM, but fitting the two-level factors of Pre-fed and Post-fed, their interaction (Pre-fed*Post-fed), Habitat (PCA scores), the interaction of each factor and habitat (Pre-fed*Habitat and Post-fed*Habitat) and a three-level interaction (Pre-fed*Post-fed*Habitat). All statistics were carried out using IBM SPSS Statistics v19.

RESULTS

Lay date was unaffected by supplementary feeding before egg laying but was positively associated with Habitat ($F_{df=1,17}$ = 5.42, P = 0.032) i.e. Buzzards nesting in poor quality landscapes with a high coverage of bog, scrub and natural grasslands typically laid later (Supporting Information Table S1 and Fig. S2). There was a trend for Buzzards that were pre-fed (i.e. before egg laying) to have slightly more (+0.6) eggs than those not pre-fed ($F_{df=1,18}$ = 3.67, P = 0.072). After removing the effect of habitat, the marginal estimated mean clutch size was 3.2 ± 0.5 eggs (mean ± 95% confidence intervals) for pre-fed pairs and 2.6 ± 0.4 eggs for birds not pre-fed. Neither mean egg volume nor weight was affected by either supplementary feeding or habitat (Supporting Information Table S1).

Both early brood size and hatching success were significantly negatively associated with Habitat ($F_{df=1,18}$ = 13.55, P = 0.002 and $F_{df=1,18}$ = 17.30, P = 0.001 respectively) i.e. the greater the proportion of the surrounding landscape that was low quality habitat, the lower the proportion of the clutch to hatch and the fewer chicks hatched overall (Table S1 and Figs. S3 & S4). Total reproductive success (i.e. the number of fledglings) was negatively associated with Habitat ($F_{df=1,18}$ = 4.37, P = 0.051), i.e. the greater the proportion of the surrounding landscape that was low quality habitat, the fewer fledglings Buzzards produced (Table S1 and Figs. S5). There was also a significant interaction effect between supplementary feeding *after* the eggs hatched and Habitat, i.e. Post-fed*Habitat ($F_{df=1,18}$ = 4.49, P = 0.048). Those pairs that had not received supplementary feeding after the eggs hatched (not post-fed), followed the overall pattern of lower reproductive success in low quality habitats. However, supplementary feeding after hatching (post-fed), significantly altered the outcome where being fed after hatching removed the negative impact of low quality habitat (Fig. 1).

DISCUSSION

153 Supplementary feeding at the pre-laying stage led to a slight increase in clutch size, but did not
154 increase egg quality i.e. there was no increase in egg volume or weight, nor any increase in
155 brood size, hatching success or numbers of fledglings. This concurs with studies on other
156 raptors (Newton & Marquiss 1981, Korpimäki & Wiehn 1998). Although food availability in
157 spring may affect clutch size, habitat quality had a greater effect on lay date and the number of
158 fledglings. These results affirm the suggestion that small-scale habitat effects are important
159 drivers of breeding success in raptors (Byholm & Kekkonen 2008). Laying date was later in
160 the season and brood size, hatching success and numbers of fledglings were lower in poorer
161 quality habitats, i.e. territories containing a greater area of bog, scrub and semi-natural
162 grassland compared to more productive, agricultural landscapes. Buzzards are typically
163 associated with pastoral agriculture where there is a high density of rabbits (Swann & Etheridge
164 1995). Landscapes composed of bog, scrub and semi-improved grasslands typically have lower
165 rabbit densities as they are less productive, have fewer hedgerows suitable for warren
166 construction and, in the case of bogs, have wet soils which are sub-optimal for burrowing.
167 Taller rank grass may also hinder hunting. Buzzards in northeast Ireland prey predominately
168 on young rabbits during the breeding season (Rooney & Montgomery 2013). Thus, delayed
169 hatching in poorer quality habitats may have prevented Buzzards from exploiting seasonal
170 peaks in prey abundance (Perrins 1970).

171 Newton (1998) emphasized two critical periods of food availability for raptors; pre-laying,
172 when females build up reserves for egg production and incubation, and post-hatching, when
173 adults provision nestlings. Absence of any general effect of supplementary feeding could be
174 interpreted as poor statistical power as a result of a relatively small sample size (given for each
175 model in the Supporting Information Table S1) and the disproportionally large effect that
176 stochastic events may have had on the outcome of the experiment. For example, siblicide
177 occurred at three nests, two of which were in treatment group 2 (fed after eggs hatched), and a

178 freshly dead chick (>5 days old) was found at the base of a tree in an exposed site in treatment
179 group 3 (fed continuously). Alternatively, the absence of any effect of supplementary feeding
180 on the numbers of fledglings could be interpreted as evidence of abundant, non-limiting,
181 naturally occurring prey (Martin 1987). This is probable for nests in productive, agricultural
182 landscapes. This is supported by the number of fledglings per pair decreasing significantly as
183 the proportional cover of territories with poor quality habitat increased. Previous
184 supplementary feeding studies have documented earlier laying date and increased clutch size
185 when territory quality is poor (Newton & Marquiss 1981) or when naturally fluctuating prey
186 availability is in a trough year (Dijkstra *et al*. 1982). However, supplementary feeding after egg
187 hatching neutralised this otherwise negative effect reversing the fortunes of Buzzards in the
188 poorest quality territories. The current study, thus, emphasises the importance of food
189 availability when provisioning chicks in sub-optimal habitats.
190 The results of this study suggest that diversionary feeding as a measure to reduce losses of
191 gamebirds to Buzzards is unlikely to dramatically increase Buzzard productivity in areas where
192 prey is not limiting and there is favourable habitat structure. Similarly, productivity is unlikely
193 to be significantly affected by an increase in prey biomass, due to novel prey in south-west
194 Ireland (Rooney & Montgomery 2013, Montgomery *et al*. 2014), or in agricultural areas where
195 prey availability (principally rabbits) is high. However, this may not be the case in sub-optimal
196 habitats (for example, upland grouse moors) where diversionary feeding during the chick-
197 rearing period may be effective in the reduction of predation on Red Grouse *Lagopus lagopus,*
198 but this benefit might be offset due to concomitant increases in Buzzard recruitment (Lees *et*
199 *al.* 2012).
200
201 This study was conducted under licences issued by the Northern Ireland Environment Agency
202 (TSE/21/10; TSE/20/10) and the British Trust for Ornithology (C/5687) and complied with the

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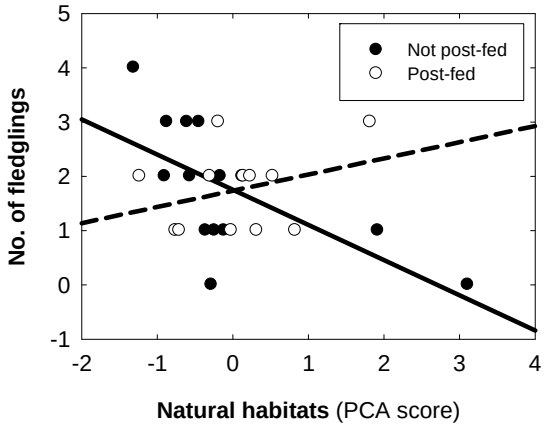

Figure 1. Buzzards nesting in low quality natural habitats e.g. bog, scrub and semi-natural grasslands (i.e. higher principal component scores on the *x*-axis) had fewer fledglings than those nesting in higher quality, agriculture landscapes except if they received supplementary feeding *after* their eggs hatched i.e. post-fed.

Natural habitat PCA scores between treatments

A General Linear Model (GLM) was conducted using the Habitat PCA scores as the dependent variable, assuming a normal distribution (tested for *a priori* using a Kolmogorov-Smirnov test) and an identity link function where there was no difference between scores between buzzard pairs that were Pre-fed and those not pre-fed ($F_{df=1,22}$ = 1.148, p=0.296; Fig. S1 *left pair*) or those Post-fed and those not post-fed ($F_{df=1,22}$ = 0.327, p=0.573; Fig. S1 *middle pair*) or with the interaction of both two-level factors i.e. the four experimental treatment groups ($F_{df=1,22}$ = 1.369, p=0.255; Fig. S1 *right four*). These results were confirmed by non-parametric Mann-Whitney U tests (U=63, p=0.297 and U=106, p=0.274 respectively) and a Kruskal-Wallis test ($\chi^2_{df=3}$ = 3.567, p=0.312). Thus by every measure, Habitat PCA scores were not confounded between the treatment groups.

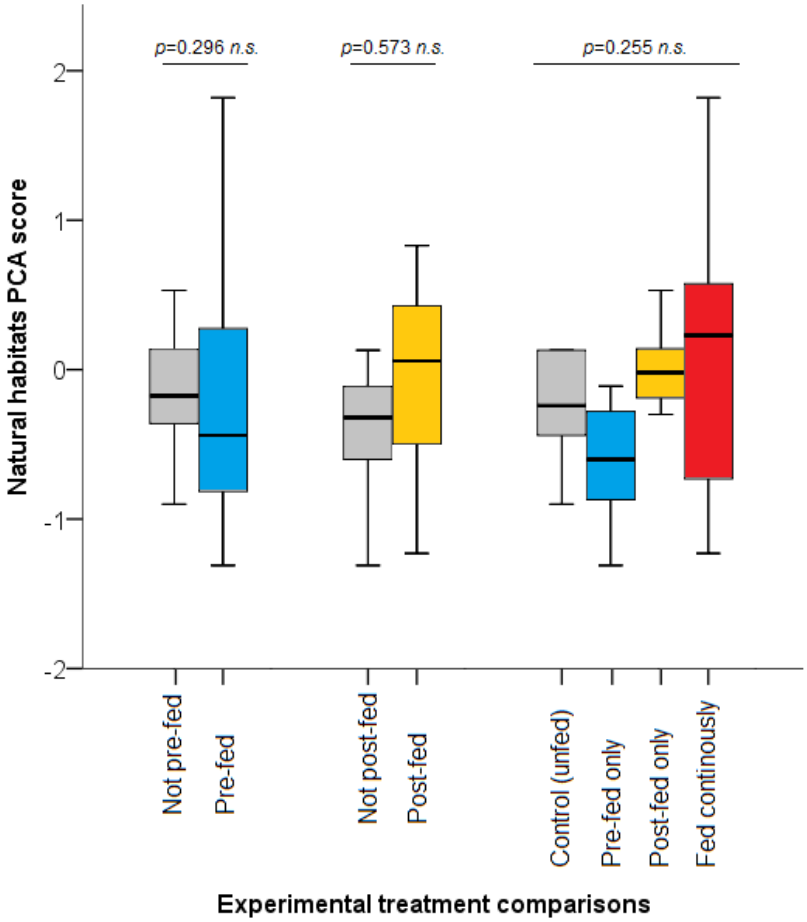

Fig. S1. Boxplot of median Habitat PCA scores between experimental treatment comparison groups.

Table S1. General Linear Models (GLMs) of response variables with experimental treatment and habitat. Significant *p*-values are shown in bold.

Model / variables	Distribution	β ± se	n.df.	d.df.	*F*	*P*
a) Lay Date (*n*=21; 9 pre-fed, 12 control)						
Pre-fed	Normal	-3.274 ± 2.608	1	17	1.576	0.226
Habitat		3.270 ± 2.685	1	17	5.423	**0.032**
Pre-fed*Habitat		Factorial	1	17	0.242	0.629
b) Clutch size (*n*=22; 9 pre-fed, 13 control)						
Pre-fed	Poisson	0.210 ± 0.110	1	18	3.666	0.072
Habitat		0.043 ± 0.110	1	18	0.001	0.972
Pre-fed*Habitat		Factorial	1	18	0.402	0.534
c) Egg volume (*n*=15; 4 pre-fed, 11 control)						
Pre-fed	Normal	2.678 ± 2.390	1	11	1.256	0.286
Habitat		2.536 ± 2.812	1	11	2.711	0.128
Pre-fed*Habitat		Factorial	1	11	0.005	0.947
d) Egg weight (*n*=15; 4 pre-fed, 11 control)						
Pre-fed	Normal	0.405 ± 3.418	1	11	0.014	0.908
Habitat		1.186 ± 4.023	1	11	0.611	0.451
Pre-fed*Habitat		Factorial	1	11	0.049	0.829
e) Brood size (*n*=22; 9 pre-fed, 13 control)						
Pre-fed	Poisson	0.103 ± 0.159	1	18	0.419	0.526
Habitat		-0.310 ± 0.152	1	18	13.552	**0.002**
Pre-fed*Habitat		Factorial	1	18	0.426	0.522
f) Hatching success (*n*=22; 9 pre-fed, 13 control)						
Pre-fed	Normal	-0.091 ± 0.098	1	18	0.875	0.362
Habitat		-0.255 ± 0.101	1	18	17.295	**0.001**
Pre-fed*Habitat		Factorial	1	18	0.073	0.790
g) Number of fledglings (*n*=26; 5 pre-fed, 5 post-fed, 7 fed continuously, 9 control)						
Pre-Fed	Poisson	-0.285 ± 0.279	1	18	3.120	0.094
Post-Fed		0.662 ± 0.483	1	18	2.811	0.111
Pre-Fed*Post-Fed		Factorial	1	18	0.533	0.475
Habitat		-0.216 ± 0.187	1	18	4.373	**0.051**
Pre-fed*Habitat		Factorial	1	18	0.284	0.601
Post-fed*Habitat		Factorial	1	18	4.494	**0.048**
Pre-Fed*Post-Fed*Habitat		Factorial	1	18	2.232	0.153

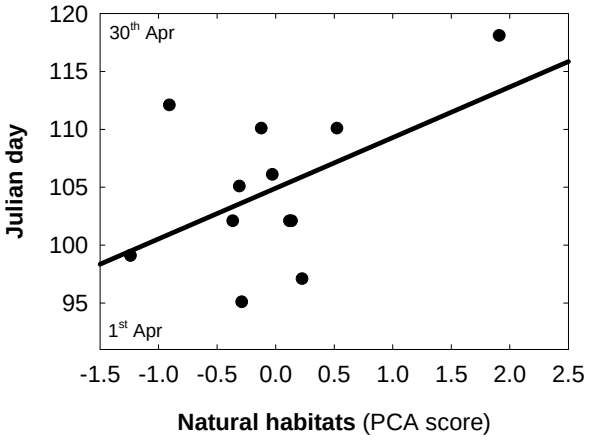

Figure S2. Buzzard pairs nesting in natural habitats (i.e. higher principal component scores on the *x*-axis) laid later than pairs nesting in anthropogenic agricultural landscapes.

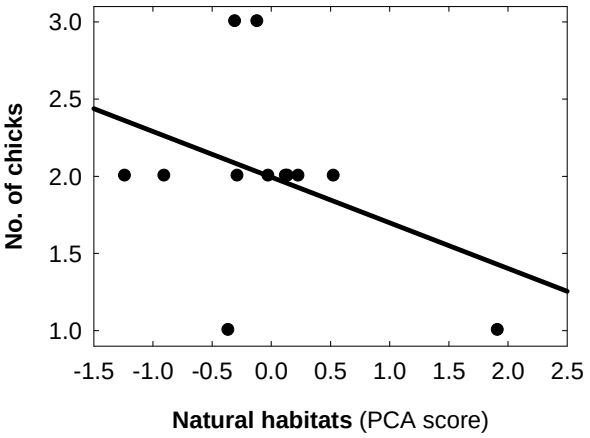

Figure S3. Buzzard pairs nesting in natural habitats hatched fewer chicks than pairs nesting in anthropogenic agricultural landscapes.

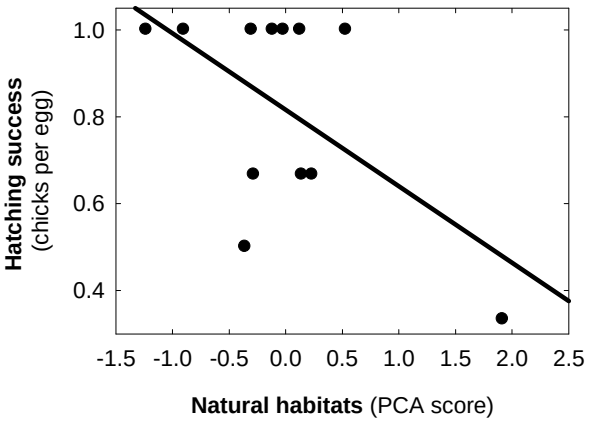

Figure S4. Buzzard pairs nesting in natural habitats had lower hatching success (chicks per egg) than pairs nesting in anthropogenic agricultural landscapes.

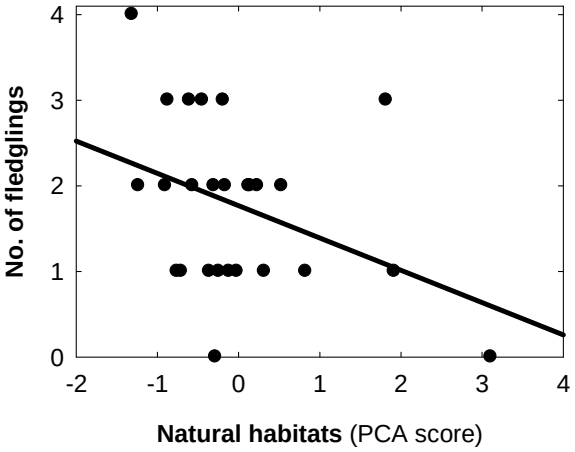

Figure S5. Buzzard pairs nesting in natural habitats had fewer fledglings than pairs nesting in anthropogenic agricultural landscapes.